THE GENERA OF GENTIANACEAE IN THE SOUTHEASTERN UNITED STATES[1]

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GENTIANACEAE A. L. de Jussieu, Gen. Pl. 141. 1789, "Gentianae," nom. cons.

(GENTIAN FAMILY)

Mostly glabrous annual, biennial, or perennial herbs [vines, shrubs, or even small trees], rarely parasitic or saprophytic. Leaves simple, opposite

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It is difficult to know where to begin to acknowledge the help of the many friends who have contributed to the preparation of this paper, for there are so many. If we can be forgiven for using a botanical figure of speech, they are all the root sources for this particular interpretation of the Gentianaceae. Although he may be appalled by this designation, the taproot of it all is Charles W. James, whose study, some 25 years ago in the very early years of the Generic Flora, produced a preliminary treatment of this family. Much information has accumulated since then. It has been possible to produce illustrations, to write and rewrite treatments of the genera, to do field work, and most gratifyingly, to see others going on to solve various taxonomic problems. In presenting this work, it has been necessary to omit a huge number of references that are connected primarily with the chemistry of compounds found in various species of *Gentiana* and of related genera of Europe or Asia.

We are most immediately indebted to Barbara Nimblett, Margaret van Montfrans, Norton Miller, and George Rogers for their multifarious help in the preparation and review of this manuscript and for various modifications of both manuscript and illustrations. We are also much indebted to Elizabeth Schmidt and Stephen Spongberg for their careful reviews and editorial help.

The initials on the illustrations will identify the artists: DHM, Dorothy H. Marsh, who was our first illustrator and who, through her special abilities, set the general style of the drawings; VS, Virginia Savage, of the thoroughly cultivated Savages of South Carolina; and KS, Karen Stoutsenberger, who worked at the Arboretum on the Generic Flora project for seven years, producing during that time more illustrations than any other artist.

The contributors of plant materials (we hope that we have not inadvertently omitted anyone) are George Avery, R. B. Channell, George R. Cooley, the late Richard J. Eaton, R. A. Howard, Robert Kral, Norton Miller, Kenneth R. Robertson, the late H. F. L. Rock, H. K. Svenson, and ourselves. Of course, the collections (both herbarium and library) of the Arnold Arboretum and the Gray Herbarium have been indispensable.

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(subopposite or verticillate), sessile, entire (rarely reduced to chlorophyllous or achlorophyllous scales), estipulate, the bases joined by a transverse line around the stem (rarely not joined but decurrent). Flowers actinomorphic [or weakly zygomorphic], perfect, mostly proterandrous. Calyx persistent, synsepalous, with 4 or 5(–14) lobes (or in *Obolaria* of 2 free, foliaceous sepals). Corolla marcescent, sympetalous, 4 or 5(–14)-parted, rotate, salverform, cylindrical, funnelform, or campanulate, frequently bearing scales or glands [or spurs], contorted (imbricate in *Bartonia* and *Obolaria*) in bud. Stamens the same number as corolla lobes and alternate with them, epipetalous; filaments distinct; anthers versatile or almost basifixed, introrse, dehiscing longitudinally [rarely apically], distinct or rarely connate. Gynoecium bicarpellate, syncarpous; style distinct or absent; stigma generally 2-lobed or 2-branched, the segments linear to orbicular or decurrent [or rarely the stigma capitate and the lobes obscure]; ovary superior, sessile or stipitate, frequently bearing glands at the base, unilocular [or rarely bilocular] with intruding, parietal [rarely axile or very rarely free-central] placentae bearing numerous anatropous ovules with one integument (the ovules straight, with the integument indistinguishable in some species of *Voyria*), less commonly with placental intrusions absent and the ovules scattered over the locule wall. Fruit a bivalvate capsule [rarely fleshy and somewhat baccate], dehiscing septicidally or rarely irregularly. Seeds with a small embryo and fleshy, nuclear (or rarely cellular) endosperm (endosperm reduced to a few cells in some species of *Voyria*). Megagametophyte (embryo sac) of Polygonum type. (Excluding Menyanthaceae Dumortier, Anal. Fam. 20, 25, 1829, nom. cons.) TYPE GENUS: *Gentiana* L.

A family of approximately 80 genera and 1100 species, essentially worldwide in distribution, but most numerous in the mountainous areas of the Northern Hemisphere and in the Andes of South America. Of the genera found in the United States, only four are not encountered in our area: *Halenia* Borkh., a genus of temperate Eurasia and North America, with one of the species, *H. deflexa* (Sm.) Griseb., widely distributed in the northern United States and southern Canada, and another, *H. recurva* (Sm.) Allen, reaching into New Mexico and Arizona; *Lomatogonium* A. Br. (*Pleurogyne* Esch.), of the North Temperate Zone, with one of the species, *L. rotatum* (L.) Fries, widely distributed in Canada and Alaska and known from a single area in Colorado; *Microcala* Hoffm. & Link, a genus of two species in the Mediterranean-type climatic areas of Europe, Africa, and the Americas, with *M. quadrangularis* (Lam.) Griseb. distributed in western Oregon and California, and disjunctively in Peru and Chile; and *Swertia* L. (*sensu stricto*), a widely distributed genus with a single species, *S. perennis* L., in North America along the Pacific coast of Alaska and Canada and in a few scattered localities in the mountains of the western United States (also Eurasia). Although never forming the dominant element, many members of the Gentianaceae are conspicuous in various vegetation types around the world, from arctic tundras to tropical savannas. Several species are among our most beautiful wildflowers, but relatively few are cultivated.

The Gentianaceae have traditionally been associated with the Loganiaceae (and segregate families), Apocynaceae, and Asclepiadaceae (and sometimes the Oleaceae, Rubiaceae, and several small families) in the orders Contortae or Gentianales. Gilg and others have considered the Gentianaceae to be most closely related to the Loganiaceae, and indeed these two families are similar morphologically. Hutchinson, however, placed the Loganiaceae, as well as the Apocynaceae and the Asclepiadaceae, in his Lignosae subphylum, far distant from the Gentianales, which in his system included only the Gentianaceae and the Menyanthaceae. Most phylogenists have agreed that the origin of the Gentianales lies in the Caryophyllales or perhaps the Saxifragales, and that they are ancestral to most of the higher, sympetalous dicots.

The family is a difficult one taxonomically. Generic limits are often poorly defined, and intergeneric relationships are not well understood. Two subfamilies have often been recognized. The Gentianoideae, by far the larger, are terrestrial (rarely saprophytic or possibly parasitic) herbs or shrubs with mostly opposite, sessile (rarely alternate or petiolate) leaves, contorted or rarely imbricated aestivation, mostly nuclear (rarely cellular) endosperm, bicollateral vascular bundles, distinct lateral corolla traces, and a radially symmetrical vascular plan in the flowers. The Menyanthoideae, a small group of five genera and perhaps 40 species, on the other hand, are aquatic or palustrine herbs with alternate, petiolate leaves, induplicate-valvate aestivation, cellular endosperm, collateral vascular bundles, fused lateral corolla traces, and a more or less bilaterally symmetrical vascular plan in the flowers.

More recent authors have considered the differences between these subfamilies to be of sufficient magnitude to warrant their separation as distinct families, and we are adopting this view. The Menyanthaceae are represented in our area by *Menyanthes* L. (*M. trifoliata* L. var. *minor* Raf. barely reaches the mountains of northwesternmost North Carolina) and by *Nymphoides* Hill (two indigenous and one naturalized species).

Chromosome numbers have been reported for approximately 250 species in 35 genera. The base numbers appear to be $x = 5, 6, 7, 9, 11$, and 13. Chromosome number is often quite variable within a genus, and certain genera as presently circumscribed include elements apparently widely disparate cytologically. Change in chromosome number appears to have played a major role in the evolution of the family. Doris Löve contended that ". . . the family Gentianaceae can be regarded as one of the most interesting cytotaxonomical objects hitherto known. Its evolution at the species level seems to have been based on the formation of abrupt species by aid of polyploidy as well as on the gradual evolution of species with the same chromosome number. The generic diversification, however, has been based in a high degree on alloploidy, as shown in the great variation in the basic numbers of chromosomes between the different groups."

Floral anatomy in the Gentianaceae has been studied by several workers. The basic vascular plan appears to be one in which the traces to the three lower series of floral organs originate in whorls, with one trace to each organ. Each of the calyx and corolla traces branches into three. The vascular cyl-

inder ultimately splits into three traces that supply the gynoecium, with one dorsal and two ventrals to each carpel. Specialization has generally tended toward fusion of traces, both within the same whorl and between whorls. Thus, in some groups the lateral traces of adjacent calyx lobes arise as single fused bundles (distinct from the median bundles); the same is sometimes true for both adjacent corolla laterals and carpel ventrals. Extreme fusion is found in certain advanced members. In these the vascular cylinder breaks up below the receptacle into a dictyostele consisting of five bicollateral bundles, each one made up of traces to each of the floral whorls.

The placentation of the gentianaceous ovary has also received considerable attention. According to Lindsey, the primitive form is unilocular, with a single row of ovules along each of the four carpel edges (the placentation parietal). Specialization seems to have been in two directions: 1) the placental zone spreading laterally, with ovules borne over most of the locule wall; and 2) placental outgrowths from the carpel edges protruding in varying degrees into the locule, in extreme cases forming bilocular ovaries with essentially axile placentation or, very rarely, unilocular ovaries with at least partly free-central placentation. Gopal Krishna and Puri argue, however, that the bilocular condition, with axile placentation, is the primitive type, and that specialization has tended in one direction toward unilocular ovaries with free-central placentation and toward parietal placentation in the other. However, Lindsey warned against attaching too much taxonomic importance to the unilocular *vs.* bilocular condition of gentianaceous ovaries. "From the morphological standpoint it is apparent that a phylogenetic or even ontogenetic change from unilocular to bilocular or *vice versa* is by no means drastic in view of the highly plastic placentae in the Gentianaceae."

Gilg's monograph (1895), the most recent of the family, was based largely on characters of the pollen grain. Tribes, subtribes, and some genera were delimited primarily on this basis. Although some of Gilg's suprageneric groups appear to be natural, many—particularly the more advanced ones—are not. Pollen morphology in the family is diverse, particularly in exine ornamentation, and is difficult to correlate with gross morphological trends. Most genera have pollen produced as single grains, but some have pollen in tetrads, and a very few have tetrads held together in polyads. Genera with pollen in tetrads or polyads, an otherwise diverse group restricted to the New World Tropics, were assembled by Gilg into a separate tribe, Helieae; other genera, which have single pollen grains but are closely related morphologically, were placed in the Gentianeae or Rusbyantheae (*Rusbyanthus*, the only genus in the Rusbyantheae, has recently been included in *Macrocarpaea* by Weaver, thus eliminating the tribe). Recent palynological studies with larger samples and more advanced techniques have suggested that a review of the alignment or the circumscription of certain genera is in order. The presence or absence of floral glands and their position and morphology have been largely ignored as important characters above the generic level. Five distinct generic groups based on glandular characteristics appear to be present in the family: 1) genera in which glands are completely absent (*Centaurium*,

Sabatia); 2) genera in which the base of the ovary is glandular, but the glands are not well developed (*Gentiana, Eustoma, Obolaria*); 3) genera in which the glands are epipetalous (*Gentianella, Gentianopsis, Frasera,* and *Swertia*); 4) genera with a well-developed glandular disc at the base of the ovary (Gilg's Gentianeae subtribes Tachiinae and Helieae, mostly woody genera of the American tropics); and 5) *Voyria*, with a number of species having two stalked glands at the base of the ovary. The trend in the Gentianales appears to be from glandless flowers to flowers with a well-developed glandular disc (except for the highly specialized Asclepiadaceae). The Gentianaceae appear to represent an intermediate stage in the evolution of glands within the order.

Growth form in the family varies from delicate ephemeral annual herbs to substantial shrubs and even weak-wooded, small trees. The woody condition appears to be a derived one. Except for the South African *Orphium frutescens* (L.) E. Meyer, all the woody members are neotropical and on the basis of other characters appear to represent a natural group. They were placed in two tribes by Gilg (1895): Gentianeae (only subtribe Tachiinae) and Helieae, but these probably should be merged. Several herbaceous genera were included here as well, and the genus *Lisianthius* P. Br. alone contains the whole range from annual plants to small trees.

All of the plants in the primarily woody groups have a well-developed glandular disc at the base of the ovary, a specialized condition in the family. The presence of pollen grains in tetrads or polyads, again an apparently specialized condition in this family, is found in most members of these groups and is restricted to them. The vascular anatomy of the flowers is the most advanced type in the family. Finally, although chromosome counts in these groups are relatively few, the chromosome numbers are uniformly high.

A meaningful classification of the Gentianaceae must take into account the gradually accumulating evidence from all sources. Since none of the existing treatments of the family appears to be completely satisfactory, infrafamilial groupings will not be considered here.

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KEY TO THE GENERA OF GENTIANACEAE IN THE SOUTHEASTERN UNITED STATES

A. Leaves mostly in whorls of 4 or 5; nectaries conspicuous, fringed, borne slightly below the middle of the corolla lobes. ..... 6. *Frasera.*

A. Leaves opposite or rarely alternate; nectaries present or absent—if present inconspicuous, not fringed, borne at base of corolla or base of ovary.

B. Calyx of 2 free, foliaceous sepals; corolla with inconspicuous scales below bases of filaments; petiole bases decurrent entire length of each internode. ..... 7. *Obolaria.*

B. Calyx of 4 or 5 (rarely to 14) nonfoliaceous segments united at least at base; corolla never with fimbriate scales; leaf or petiole bases joined, forming a green or scarious sheath around stem, very rarely weakly decurrent.

C. Leaves well developed, never scalelike, always opposite; plants green and obviously autotrophic.

D. Style filiform; ovary sessile.

E. Corolla rotate, 5–12(–14)-parted; stigma lobes linear or spathulate, spirally twisted at anthesis but later uncoiling and spreading. ..... 1. *Sabatia.*

E. Corolla salverform or campanulate, 4- or 5-parted; stigma lobes elliptic or orbicular, never spirally twisted.

F. Corolla salverform, tube longer than calyx; anthers becoming spirally twisted upon dehiscence. ..... 2. *Centaurium.*

F. Corolla campanulate, tube shorter than calyx; anthers remaining straight after dehiscence. ..... 9. *Eustoma.*

D. Style short and stout, sometimes barely discernible; ovary stipitate.

G. Corolla 5-parted, with plicate appendages in sinuses of lobes; nectaries on base of gynophore. ..... 3. *Gentiana*.
G. Corolla 4- or 5-parted, without plicate appendages in sinuses of lobes; nectaries on base of corolla, alternating with the stamens.
H. Corolla 5-parted, lobes entire, erect; flowers sessile or short-pedicellate. ..... 4. *Gentianella*.
H. Corolla 4-parted, lobes ciliate, spreading; flowers long-pedicellate. ..... 5. *Gentianopsis*.
C. Leaves scalelike, alternate or opposite; plants slender, green to colorless, semisaprophytic or semiparasitic.
I. Flowers 4-merous; plants with chlorophyll; aestivation of corolla imbricate; stigmas decurrent along style to top of ovary. .. 8. *Bartonia*.
I. Flowers 5-merous; plants without chlorophyll; aestivation of corolla convolute; stigmas capitate or peltate. ..... 10. *Voyria*.

1. **Sabatia** Adanson, Fam. Pl. **2:** 503. 1763.

Erect, glabrous, annual, biennial, or perennial herbs (the perennials sometimes stoloniferous), arising from branched rhizomes or rarely from a short, erect caudex. Roots fibrous, fleshy, or wiry, or some annual species with a slender taproot. Leaves decussate, cauline (but also in a basal rosette in some species), sessile and sometimes clasping, membranaceous to fleshy. Flowers large to quite small, sessile or long-pedicellate, subtended by scalelike or rarely foliaceous bracts, solitary or more commonly in few-flowered monochasia or conical, flat-topped, or subcapitate clusters of dichasia. Calyx 5–12(–14)-lobed, persistent, the tube campanulate to somewhat turbinate, the lobes minute to foliaceous. Corolla rotate, marcescent, often showy, white or various shades of pink to purple, often with a conspicuous yellow "eye" or "star" in the throat, the 5–12(–14) lobes much longer than the tube, dextrorsely convoluted in bud. Stamens 5–12; filaments slender, adnate to the upper edge of the short corolla tube; anthers basifixed, linear to oblong, dehiscing laterally by longitudinal slits, becoming circinately coiled or rarely only recurved or slightly twisted laterally after pollen discharge. Stigma 2-branched, the branches linear or slightly spathulate, tightly spirally twisted and bent to one side at anthesis, but later untwisting and becoming erect or recurved; style slender, ovary unilocular, the slightly intruded carpel margins forming 4 parietal placental lobes with numerous ovules. Capsule subglobose to cylindrical; seeds numerous, globose or somewhat flattened, densely pitted. (Including *Lapithea* Griseb.) TYPE SPECIES: *Chironia dodecandra* L. = *Sabatia dodecandra* (L.) BSP. (Name commemorating Liberato Sabbati, eighteenth-century Italian botanist who published on the plants of Rome.)

A North American genus, primarily of the Atlantic and Gulf coastal plains of the southeastern United States, but extending northward into Nova Scotia and westward to Michigan, Kansas, Oklahoma, and central Texas, and southward into central Mexico (on the west) and from southernmost Florida to the Bahamas, Cuba, and Hispaniola (on the east). All of the eighteen species (two composed of two varieties) occur in the Southeast; four are not found outside this area.

Infrageneric groups in *Sabatia* appear to be well defined in most cases,

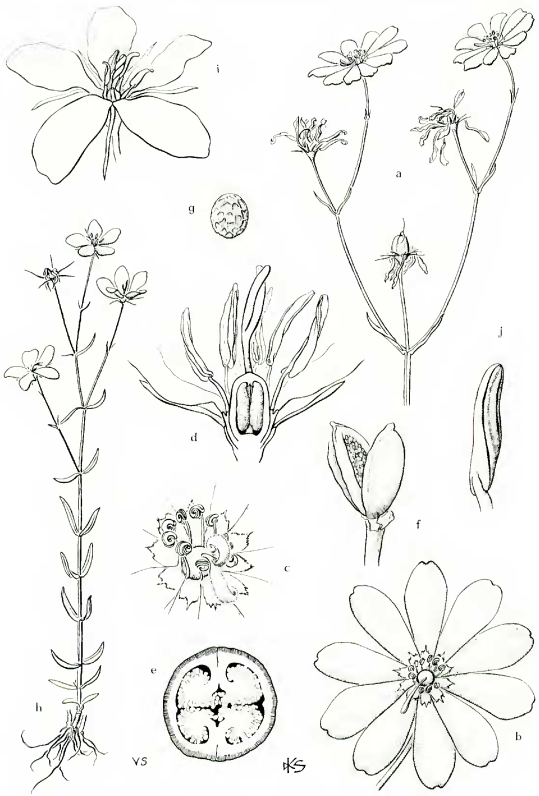

FIGURE 1. **Sabatia.** a–g, *S. Kennedyana*: a, inflorescence with flowers and partly mature fruit, × ½; b, flower, pollen shed, stigmas not yet expanded, × 1; c, detail of flower, showing recurved anthers and receptive stigmas, × 2; d, off-center vertical section of flower at anthesis, the ovary cut to show numerous ovules on two parietal placentae, × 3; e, cross section of ovary, showing placentation, × 6; f, dehiscing

but the rank of a few of these has been debated. Members of sects. SABATIA (13 species) and CAMPESTRIA J. D. Perry (three species) have in common pedicellate flowers borne either singly or in loose cymes and subtended by scalelike bracts, with the anthers becoming circinately coiled as the pollen is discharged. Within sect. SABATIA, Wilbur (1955) recognized five subsections, one of which (*Campestres* Blake) was later raised to sectional rank by Perry (1971) on the basis of both morphological and crossing data. A third section, PSEUDOCHIRONIA Griseb., composed of two well-marked species, has been generally recognized and sometimes raised to the rank of genus (*Lapithea* Griseb.).

Annuals, biennials, and perennials with alternate to opposite branching and with affinities to a wide variety of habitats (dry to wet, fresh to salt water) are represented in sect. SABATIA. Various species have 5–12(–14) corolla lobes, and haploid chromosome numbers of 13, 14, 16, 17, 18, 19, 20, 32, and 38 are known (along with two aneuploid races in *S. quadrangula* [$2n = 32, 34$]). The anthers are either recurved or circinately coiled after pollen release, and the stigmatic branches are usually coiled when receptive. *Sabatia angularis* (L.) Pursh, $2n = 38$, of subsect. *Angulares*, is the most widespread and familiar species of the genus. Subsection *Dodecandrae* Wilbur (four species of rhizomatous perennials with pink, mostly plurimerous flowers and alternate branching) was considered by Blake to be worthy of sectional rank (sect. *Pleienta* (Raf.) Blake). Both *S. dodecandra* (type species of the genus) and *S. Kennedyana* Fern. (widely disjunct between Nova Scotia, eastern Massachusetts and Rhode Island, and southeastern North Carolina and northeastern South Carolina) belong here.

In Wilbur's excellent revision of *Sabatia*, *S. campestris* Nutt., $2n = 26$, and *S. arenicola* Greenman (including *S. carnosa* Small), $2n = 28$, constitute subsect. *Campestres* Blake. Both species, which have more westerly distributions than others in the genus, are annuals with pink, pentamerous flowers, a predominantly five-veined and thinly winged calyx tube, and alternate branching. In an extensive biosystematic study of the genus, Perry (1967, 1971) found that all artificial crosses between the two species were unsuccessful, as were all crosses between them and other species of the genus. The lack of crossability suggested to Perry greater divergence than would be implicit in only subsectional status. He concluded that the closest relatives appear to be the species of subsect. *Angulares*. More recently, Bell and Lester (1978, 1980) presented morphological and allozymic evidence for recognition of a third species in the section, *S. formosa* Buckley (first recognized in 1862), which is very similar to *S. campestris* and which had been merged with it. They also discovered a cline of variation between *S. arenicola* and *S. formosa* that they attributed to introgressive hybridization resulting from "hybridization of the habitat."

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capsule, the marcescent perianth and androecium removed, × 3; g, seed, × 25. h, *S. campanulata*, flowering plant, × ½. i, *S. difformis*, flower showing recurved (rather than coiled) anthers, × 2. j, *S. gentianoides*, dehiscing anther, × 6.

Section PSEUDOCHIRONIA Griseb. (*Lapithea* Griseb.) includes only two very distinctive species, both perennials (see Perry) with pink, 7–12-lobed corollas. Both differ from species of sects. SABATIA and CAMPESTRIA in their nearly sessile solitary or capitate flowers subtended by foliaceous bracts, and in their anthers that become only slightly twisted laterally upon pollen discharge. Geographically the most restricted of all the species of *Sabatia*, and the only one that is not found on the Coastal Plain, *S. capitata* (Raf.) Blake, $2n = 76$, is a rare plant of open hardwood forests on hillsides and ridges in the Appalachians of northwestern Georgia, southeastern Tennessee, and northern Alabama.

Easily distinguished from the preceding species by its dimorphic leaves, subulate (rather than linear) calyx lobes, and distribution, *Sabatia gentianoides* Ell., $2n = 28$, is found in pinelands and savannas on the Coastal Plain from northern North Carolina south and west to eastern Texas (rare in peninsular Florida). The chromosome numbers of these species represent extremes in the genus, and repeated artificial crosses between them have failed. However, seed-set was high when both were crossed with various species in sect. SABATIA subsect. *Dodecandrae*; *S. gentianoides* also crossed with several species of sect. SABATIA subsect. *Campanulatae*, although only the cross with *S. grandiflora* produced a high seed-set. Progeny from only one of the crosses (*S. gentianoides* × *S. Bartramii*) were grown to maturity, and in those pollen viability was very low. The crossing experiments suggest that the species of this section are most closely related to those of sect. SABATIA subsect. *Dodecandrae*.

The basic chromosome number in *Sabatia* is thought to be $x = 7$, the present array of numbers resulting from a remote and now concealed polyploidy, with subsequent aneuploid reduction and secondary polyploidy. Although not necessarily operating at the level of initial crossability, difference in chromosome number is a barrier to hybridization in the genus. "While heteroploid crosses do not give a true indication of genetic relationship, they show that aneuploidy has been an effective source of caryological variation leading to reproductive isolation among closely related species and, presumably, to species formation" (Perry, 1971). Corresponding to a decrease in chromosome number are tendencies toward an annual or biennial habit and simplification of morphology (including decrease in floral size, number of floral parts, and prominence of leaves).

The breeding system is primarily allogamous. The flowers of most species are proterandrous, the anthers twisting or recurving as the pollen is shed. The two stigmatic branches are "tightly spirally twisted at anthesis and bent to one side, later becoming erect, untwisting and exposing the densely papillate stigmatic surface" (Wilbur). In the proterandrous species, the anthers and stigmas of a single flower are not brought into direct contact. However, in the relatively unrelated *Sabatia calycina* and *S. arenicola* (both species of unstable habitats), the stigmatic surfaces are receptive on the same day that the pollen is released. In addition, the anthers and stigmas are brought into direct contact, assuring autogamy in these two species. The latest-ma-

turing flowers of *S. difformis* and *S. macrophylla* are frequently staminate due to arrested development of the gynoecium, but the effect of this staminate expression on out-crossing is thought to be negligible. Polylectic bees have been shown to be the primary pollinators of *Sabatia* species: *Bombus* (Apidae) in the case of the large-flowered ones, and smaller bees (usually Halictidae) in the others.

Although vigorous (but usually sterile) first-generation hybrids between many of the species have been produced artificially, instances of natural hybridization in *Sabatia* are unknown, even though as many as five species have been found in the same general area. In nearly all cases involving sympatry, however, the species concerned are not intercrossable. (See Perry.)

Although most of the species of *Sabatia*, particularly the plurimerous ones, have attractive and colorful flowers, none seems to be cultivated. The genus has been placed most often near *Centaurium* Hill (*q.v.*), from which it is distinguished by the rotate corolla and characters of the stigma and anthers.

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2. **Centaurium** Hill, Brit. Herbal. 62. 1756; Adanson, Fam. Pl. **2:** 502. 1763, "Centaurion."

Annual or biennial [rarely perennial] herbs. Roots fibrous [or rarely forming a slender taproot]. Stems sparingly to profusely branched from above or below, terete or quadrangular [or 4-winged] in cross section. Leaves cauline or the lower ones arranged in a basal rosette in the biennial species, sessile, opposite, often clasping, with 1–3 veins from the base. Flowers (4- or) 5-merous, rose, pink, or rarely white [or very rarely yellow], without obvious

glands, [solitary or] borne in loose or congested cymes. Calyx persistent, deeply divided into (4 or) 5 slender, carinate lobes. Corolla marcescent, salverform, with an elongate tube [to subrotate, with a short tube, or rarely funnelform], the (4 or) 5 lobes patent, dextrorsely contorted in bud. Stamens (4 or) 5, inserted on the upper part of the corolla tube; filaments filiform; anthers often exserted, introrse, erect, oblong to linear, spirally twisted after anthesis. Stigmas 2, [linear to] oblong, reniform, or flabelliform, sometimes the stigma solitary, with 2 distinct lobes [or rarely the lobes confluent and the stigma subcapitate]; style filiform, bifid at apex or simple, deciduous; ovary unilocular, the 2 bilobed placentae often much intruded, each lobe with several rows of ovules. Capsule oblong to fusiform, the placentiferous margins of the valves often intruded and involute. Seeds numerous, minute, subpyramidal to suborbicular, brown or pale brown [or sometimes nearly black], finely foveolate-reticulate. (*Erythraea* Borkh.) TYPE SPECIES: *Gentiana Centaurium* L. (see Britton & Brown, Illus. Fl. No. U. S. Canada **3:** 1. 1913) = *Centaurium littorale* (D. Turner) Gilmour (see Gillett, The gentians of Canada, Alaska, and Greenland, 78, 79. 1963). (Name from Latin *centaureum* [Greek, *kentaurion*], the ancient name of a red-flowered plant, possibly *Centaurium Erythraea,* the medicinal properties of which were supposed to have been discovered by Chiron, the centaur who tutored Achilles, Hercules, and Asclepius.)—CENTAURY.

A taxonomically difficult genus of approximately 100 described species, nearly cosmopolitan in distribution except for tropical and southern Africa. Four sections have been recognized by Grisebach, Gilg, and others, and two of these include species native to North America. Most of the 25 or so North American species are distributed in Central America, Mexico, and the western United States. Two or three of these barely reach the western part of our area, and two or possibly three more introduced European species are sporadic in the eastern portion. All except the adventive *Centaurium spicatum* (L.) Fern. are referable to section CENTAURIUM.

The typical variety of *Centaurium Beyrichii* (Torrey & Gray) Robinson is a plant of calcareous slopes and granitic rocks in Texas, Oklahoma, and Arkansas; var. *glanduliferum* Correll is restricted to western Texas. Another calciphile, *C. texense* (Griseb.) Fern. is recorded from central and southwestern Missouri, northern Arkansas, western Louisiana, and Texas. The widespread typical variety of *C. calycosum* (Buckley) Fern. is common from Texas throughout the Southwest. It has been recorded from Jackson County, Missouri (where it is possibly introduced), and is to be looked for in Arkansas; var. *breviflorum* Shinners is restricted to central and southern Texas.

Centaurium Erythraea Rafn (*Gentiana Centaurium* of authors, not L.; *Erythraea Centaurium* of authors, not (L.) Borkh.; *C. minus* of authors, not Moench; *C. umbellatum* of authors), $2n = 20, 40, 42$, is indigenous to all but the northernmost parts of Europe. It is a variable plant, and six subspecies have been recognized on the basis of various morphological features, as well as chromosome number. It has been reported as adventive in a number of

localities in the United States and Canada. Within our area it has been reported from North Carolina and doubtfully from Georgia and is to be looked for elsewhere.

There is considerable confusion as to the application of Linnaeus's name *Gentiana Centaurium,* and therefore the typification of the genus. The name has most commonly been applied to this species. We are following Dandy, who (as reported by Gillett) pointed out that the type of *Gentiana Centaurium* L. is actually the plant now known as *C. littorale* (D. Turner) Gilmour. Dandy rejected the name *C. minus* Moench (which until that time was widely accepted as the correct name for this species, but based on *Gentiana Centaurium* L.) under Article 65 of the *International Code of Botanical Nomenclature* as having been consistently misapplied.

Another widespread European species, *Centaurium pulchellum* (Sw.) Druce, $2n = 20, 36, 40, 42, 54, 56$, has been recorded from southern Virginia, Mississippi, and Louisiana. *Centaurium spicatum* (L.) Fritsch, $2n = 22$, distinctive in its spiciform inflorescence, is native to southern Europe. It has been collected beyond our range from Virginia to Massachusetts and should be looked for in the Southeast.

Many of the species are quite variable. Taxonomic characters include inflorescence type; proportions and sizes of corolla lobes and tubes, insertion of stamens, shape of stigmas, and shape of leaves. Although various regional treatments exist, a modern monograph of the genus is much needed.

Centaurium is presumably most closely related to *Sabatia,* from which it is readily distinguished by the salverform (as opposed to rotate) corollas and the spirally twisted (rather than coiled) or recurved anthers.

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3. **Gentiana** Linnaeus, Sp. Pl. **1:** 227. 1753; Gen. Pl. ed. 5. 107. 1754.

Glabrous or puberulent perennial [annual or biennial] herbs, with 1 to several [to many] simple or sparsely branched stems and stout, often yellowish roots from a short caudex [or plants rhizomatous with fibrous roots, or annual species with stems often branched from base and with fibrous roots or weak taproots]. Leaves opposite [very rarely verticillate], cauline, often gradually reduced below, the lowermost scalelike [or the lower ones in a loose to dense rosette and either similar to or quite different in shape from the cauline ones], the upper pairs often congested and appearing involucrate about the flowers. Flowers sessile or pedicellate, solitary or in simple dichasia, these often congested in dense terminal and/or axillary clusters. Calyx [4 or] 5 [or 6]-lobed, the lobes minute and toothlike to subfoliaceous, connected by a membrane continuous around the inner rim of calyx tube [or the intracalycine membrane very rarely absent], [tube occasionally split down 1 side and calyx then spathiform, or split down 2 sides and calyx 2-lipped]. Corolla marcescent, [4 or] 5 [or 6]-lobed, funnelform to broadly cylindrical or fusiform [or rotate, campanulate, salverform, or obconical]; the lobes spreading to erect or incurved, large to obsolescent; the tube with plicate appendages (plaits, pleats) between the lobes, these asymmetric [or symmetrical], [entire or] variously toothed or divided, retuse to lacerate, shorter (rarely longer) than corolla lobes [or rarely obsolescent]. Stamens [4 or] 5 [or 6]; filaments often winged, adnate to corolla tube, the adnate portions decurrent; anthers free at anthesis or connate, introrse, or becoming pendent and then extrorse. Gynoecium stalked [or sessile], the gynophore glandular at base [or if sessile, glands at base of ovary], glands as many as corolla lobes; ovary bilocular, fusiform to ovoid or ellipsoid, the numerous ovules scattered over most of inner surface of ovary [or organized into 4 distinct vertical zones]; styles short and stout [or slender] or stigma sessile; stigma deeply bilobed [or lobes connate into a roundish disc], the lobes subulate [or roundish]. Capsule stalked [or sessile], protruding from or enclosed by the marcescent corolla, 2-beaked. Seeds numerous, roundish [or elongate], smooth [or striate or alveolate], broadly or narrowly winged all around [or wingless]. Lectotype species: *Gentiana lutea* L.; see Adanson, Fam. Pl. **2:** 503. 1763. (Name from Gentius, King of Illyria, who supposedly discovered medicinal properties in the plants.)—Gentian.

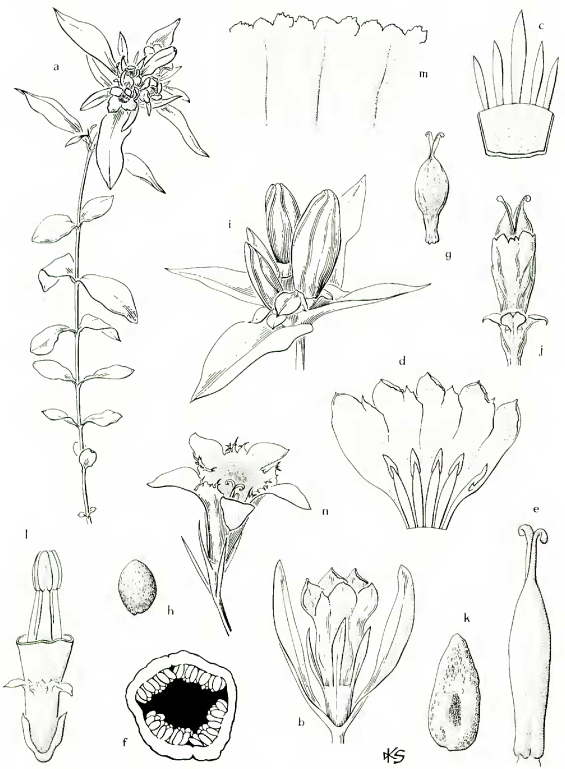

FIGURE 2. **Gentiana.** a–h, *G. villosa*: a, flowering stem, × ⅓; b, flower with subtending bracts, × 1; c, opened calyx (abaxial lobe longest) seen from within, showing intracalycine membrane, × 1; d, opened corolla, showing stamens and plaits, × 1; e, gynoecium with nectariferous lobes at base of ovary, × 2; f, cross section of ovary, showing placentation, × 6; g, nearly mature capsule, × 1; h, seed (wingless), × 12. i–k, *G. clausa*: i, tip of flowering stem, × 1; j, mature fruit with marcescent corolla (note plait between corolla lobes—two lobes of plait unequal), × 1; k, seed (winged),

Gentiana is here accepted in its restricted sense; that is, the group corresponding basically to Kusnezow's subgenus EUGENTIANA and distinguished from *Gentianella* Moench (subgen. GENTIANELLA Kusn.) by the presence of nectaries around the base of the ovary or on the gynophore (rather than on the corolla tube), plaited appendages between the corolla lobes (these occasionally greatly reduced, or absent in *G. lutea,* the type of the genus), and (usually) a rim or membrane extending completely around the interior of the calyx tube. Even in this restricted sense, *Gentiana* is a large, polymorphic, and taxonomically difficult genus. Kusnezow, the most recent monographer, recognized 161 species, but Marquand later listed 184 species for China alone. The genus occurs primarily in arctic and montane areas of the Northern Hemisphere, with one to three species crossing the Equator in Andean South America and a few in the large islands of Indonesia.

All of the species of *Gentiana* in our area belong to section PNEUMONANTHAE Bunge, a group of 40 to 50 species widespread in Eurasia and North America. The plants of this section are perennials with one to several stems arising from a short rootstock; a well-developed intracalycine membrane; conspicuous, symmetrical or asymmetric, more or less bifid corolla plicae with erose or laciniate apices; flattened seeds completely surrounded by a membranaceous wing; and a diploid chromosome number of 26 (except for the European *G. asclepiadea* L., which is probably misplaced here). About 25 species are found in North America, with two more or less distinct areas of distribution, one in the western mountains from Alaska to Mexico, the other in the eastern woodlands and prairies. The species of eastern North America have been treated most recently by Pringle, who recognizes 11 species in our area. Only one of these is restricted to the Southeast, but seven others are primarily Southeastern in distribution.

Two distinct groups are recognizable within the Southeastern species of sect. PNEUMONANTHAE. *Gentiana autumnalis* L. (*G. Porphyrio* J. F. Gmelin), $2n = 26$, a plant of sandy meadows and pine woods on the Atlantic Coastal Plain from central New Jersey to south-central South Carolina, and *G. Pennelliana* Fern., an endangered species restricted to open sandy sites in western Florida (Bay, Gadsden, and Wakulla counties), are distinctive in their narrow, often linear leaves, solitary pedicellate flowers, and open, campanulate corollas with spreading lobes that far exceed the plicae (plaits or pleats). The two were segregated by Clausen as subsect. *Angustifoliae,* a taxon that has not commonly been accepted. As Pringle (1967) pointed out, the subsection was based solely on a consideration of American species; moreover, these species are "much more similar to *G. pneumonanthe* [the type of sect. PNEUMONANTHAE] than are most of the North American species left in the nominate subsection."

× 12. l, m, *G. austromontana*: l, flower with upper part of corolla removed to show connivent stamens, × 2; m, three corolla lobes (corolla opened out flat, the corolla lobes with veins) and plaits between (plaits with two equal lobes), × 2. n, *G. autumnalis*, flower, × 1.

The remaining species are characterized by broader leaves; clustered, involucrate, sessile or subsessile flowers; and broadly funnelform or cylindrical corollas that are closed at anthesis or occasionally have spreading lobes. The "bottle gentians" belong here. One of the most widespread and familiar of the Southeastern species, *Gentiana Saponaria* L. (*G. latifolia* (Chapman) Britton and including *G. cherokeensis* (Lemmon) Fern.), $2n = 26$, is a plant of moist or seasonally wet thickets, open woods, and roadsides from eastern Long Island, south along the Atlantic Coastal Plain to northeastern North Carolina, then through the Piedmont of the Gulf States from northwestern Florida to southeastern Texas, north to southeastern Oklahoma and northwestern Illinois (mostly absent from the Appalachians). According to Pringle (1967), *G. Saponaria* var. *latidens* House, from the mountains of western North Carolina, is a hybrid between *G. clausa* and *G. decora*.

Similar to the preceding but more coastal in distribution, *Gentiana Catesbaei* Walter (*G. Elliottii* Chapman, *G. parvifolia* (Chapman) Britton) is found in open woodlands, clearings, and roadsides on the Atlantic Coastal Plain from northern New Jersey to northern Florida. It differs from *G. Saponaria* in its broader leaves, longer calyx lobes, and longer and more spreading corolla lobes. Although these species are sympatric to some degree, and their habitats are apparently similar, clear-cut instances of hybridization are rare.

The montane counterpart of *Gentiana Saponaria*, *G. decora* Pollard, $2n = 26$, is distributed in mesic woodlands at higher elevations from northeastern Georgia through western North and South Carolina and eastern Tennessee, to southwestern Virginia, with an outlier in northeastern West Virginia. This species differs from *G. Saponaria* in its smaller, paler, and more open flowers, its asymmetric corolla plicae, and its shorter, subulate calyx lobes. Hybridization between *G. decora* and *G. Saponaria* has been suspected in at least one instance.

Primarily a prairie species, *Gentiana puberulenta* Pringle (*G. puberula* of authors), $2n = 26$, barely enters our area. Its distribution is in a roughly triangular area from southern Manitoba to western New York and extreme northwestern Arkansas. An outlying locality in central Louisiana (Rapides Parish) is several hundred miles distant from the nearest known populations (northwestern Arkansas). With its rather open flowers, relatively large corolla lobes, and anthers free at anthesis, this is one of the most distinctive eastern species. Until recently *G. puberulenta* has been known as *G. puberula* Michaux, but Pringle (1966) found that Michaux's type is really *G. Saponaria*.

A plant primarily of the northeastern United States, *Gentiana clausa* Raf., $2n = 26$, extends southward along the Appalachians to northeastern Tennessee and western North Carolina. It is similar to and has often been confused with the extralimital *G. Andrewsii* Griseb. It differs from all of the preceding species in that its corolla lobes are shorter than or equal to the appendages (plicae). Some specimens from the mountains of western North Carolina appear to be hybrids between *G. clausa* and the sympatric *G. decora*.

Similar to *Gentiana clausa*, but with a more slender corolla, shorter filaments, and puberulous stems and calyx lobes, the recently described *G. austromontana* Pringle & Sharp is a plant of higher elevations in the mountains of southern Virginia, northeastern Tennessee, and western North Carolina. A few collections appear to be intermediate between this and *G. decora*.

Gentiana linearis Froel., $2n = 26$, very rare in our area, is primarily a plant of boreal and subarctic areas, from southern Labrador and the eastern shore of James Bay, south to northern West Virginia and central New Jersey, with outlying populations around Lake Superior and in eastern Tennessee (Sevier County). It can be distinguished from other gentians of our area by its narrow involucral leaves and its obliquely triangular corolla plicae. The extralimital subsp. *rubricaulis* (Schwein.) Gillett is sometimes treated as a distinct species, *G. rubricaulis* Schwein.

The last two species differ from the others in their whitish or green-veined (rather than blue or purple, or blue- or purple-veined) corollas. Primarily a prairie species, *Gentiana alba* Muhl. (*G. flavida* A. Gray) barely enters our area. It is distributed from eastern Pennsylvania and southern Ontario, west to central Minnesota, and south to northwestern Arkansas, with a few populations in the southern Appalachians to Watauga County, North Carolina. Numerous hybrids (*G.* × *Curtisii* Pringle) between this species and the largely sympatric but quite different *G. puberulenta* have been reported. Hybrids between *G. alba* and *G. Andrewsii* have been named *G.* × *pallidocyanea* Pringle.

Widespread and familiar in the southeastern United States, *Gentiana villosa* L., $2n = 26$, is a plant of mesic woodlands throughout the area south of the Ohio River and east of the Mississippi, except for peninsular Florida. It can be distinguished from *G. alba* by its ecarinate calyx lobes and its dark green leaves. A specimen from Gadsden County, Florida, appears to be a hybrid between this and *G. Catesbaei*.

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4. **Gentianella** Moench, Methodus Pl. 482. 1794, nom. cons.

Mostly glabrous, annual [biennial or perennial] herbs [or rarely subshrubs]. Stems simple below and sparsely branched above [or several to many stems from the base in some perennials], [terete or] quadrangular and the angles winged at least below. Lower leaves [sessile or] tapering to an indistinct petiole and forming a loose rosette [or the rosette dense to absent], often withering before anthesis [but persistent in some perennial species]; principal cauline leaves opposite, sessile and [often] somewhat clasping, prominently [3 or] 5–7-veined [or the venation indistinct]. Flowers [4- or] 5-merous, borne in terminal and axillary umbelliform cymes [or in dichasia, or the flowers solitary, or the plants rarely subscapose]. Calyx persistent, [4- or] 5-lobed, the lobes imbricate in bud, subequal [or unequal or rarely reduced to teeth but then the calyx splitting down 1 side to form a spathiform sheath], the tube well developed, without an inner membrane, the squamellae borne at the very base in sparse tufts opposite the lobes [or in a ± continuous uniseriate ring]. Corolla funnelform [or cylindrical, salverform, rotate, or rarely campanulate], the lobes dextrorsely convolute in bud, erect [or spreading] at anthesis, the tube unornamented in the throat [or with vascularized filiform appendages, or fimbriae, these scattered, united into a continuous ring, or arranged in a row along the base of each corolla lobe; occasionally the lower part of the tube pilose inside] but with glands alternate with the stamens near the base, these glands cushionlike, crescent shaped [to deeply bifid]. Stamens included, inserted on the corolla tube at the middle or below; filaments filiform [or subulate], glabrous [or with minute papillae, or occasionally barbate below]; anthers ± versatile, introrse, but reflexing and becoming pendent and extrorse upon dehiscence [or basifixed and remaining erect in a few species]. Gynoecium stipitate [or sessile]; stigma 2-lobed, sessile [or nearly so]; ovary cylindrical [or fusiform], unilocular, the numerous ovules borne on weakly intruded placentae, these in pairs along each suture. Seeds smooth, globose [or slightly flattened], wingless. (*Gentiana* L. subg. *Gentianella* Kusn.; *Amarella* Gilib., nom. rejic.) TYPE SPECIES: *Gentianella tetrandra* Moench = *Gentianella campestris* (L.) Borner (*Gentiana campestris* L.). (Name a diminutive of *Gentiana*.)

A genus of perhaps 250 species, nearly worldwide in distribution (absent from Africa) with concentrations in the North Temperate and Arctic zones of Eurasia and North America, and in the Andes of South America (where Gilg recognized 182 species, and Macbride 97 species in Peru alone). Of the several species in the United States, only *Gentianella quinquefolia* (L.) Small, stiff gentian, ague-weed, $2n = 36$, of sect. ARCTOPHILA (Griseb.) J. Holub is found in our area. Two allopatric subspecies (or varieties) of *G. quinque-*

folia have generally been recognized: subsp. *quinquefolia* (with narrowly triangular, hyaline-margined, distinctly keeled calyx lobes 2–2.5 mm long), distributed from southern Maine to western New York, then southward along the Appalachians to northern Georgia; and subsp. *occidentalis* (A. Gray) Gillett (with elliptic-lanceolate to oblanceolate, thick-margined, indistinctly keeled calyx lobes 5–6 mm long), distributed from extreme southern Ontario and northern Ohio, west to south-central Minnesota, and south to northwestern Arkansas and southeastern Kentucky.

Gentianella has been included in *Gentiana* L. by most authors, usually as subg. GENTIANELLA Kusn. However, its relatively large number of distinctive characters, in this portion of the family where generic limits are particularly fuzzy, argue strongly for maintaining it as a distinct genus. The most obvious difference separating *Gentianella* from *Gentiana* is the absence of plicae or folds (plaits, pleats) in the sinuses of the corolla (these are greatly reduced in a few species of *Gentiana,* and generally absent in *G. lutea,* the type of *Gentiana* sensu stricto). In addition, the species of *Gentiana* are characterized by a membranaceous ring of tissue extending completely around the inner rim of the calyx tube (except in *G. Douglasiana* Bong., from western North America), while in *Gentianella* this intracalycine membrane is completely absent. Finally, the nectariferous glands are borne on the base of the ovary or the gynophore in *Gentiana,* and on the corolla tube in *Gentianella.* This last character is perhaps the most significant one. It is the only one that is entirely constant, and as pointed out by both Gillett and Toyokuni, it suggests that *Gentianella* is more closely related to *Swertia, Halenia,* and *Lomatogonium,* all of which have epipetalous glands or spurs, than to *Gentiana.*

Kusnezow (in Gilg, 1895) recognized nine sections in his subg. GENTIANELLA. Of these, sects. IMAICOLA Griseb. and CROSSOPETALUM Froel. ex Griseb. are now referable to *Gentianopsis* Ma, and sects. MEGACODON Hemsley and STYLOPHORA Clarke to *Megacodon* (Hemsley) H. Sm. The remaining five sections constitute *Gentianella* in its strictest sense, still a large and complex group that has never been monographed in its entirety. The typical section, GENTIANELLA (sect. *Amarella* (Griseb.) Gillett), contains most of the species of the North Temperate Zone as well as a few in the mountains of tropical America. These are annuals with salverform corollas that are usually fimbriate in the throat. The much smaller, but still primarily North Temperate, sect. ARCTOPHILA (Griseb.) J. Holub (to which *G. quinquefolia* belongs) also contains annual species, but those with salverform or funnelform corollas are not fimbriate in the throat. Gillett, in his treatment of the North American species of *Gentianella,* reduced these sections to series of sect. *Amarella* (GENTIANELLA). The fimbriae in the throat of the corolla are not constant, and corollas of *G. Wislizenii* (Engelm.) Gillett (which Gillett placed in his series *Arctophilae*) vary from efimbriate to densely fimbriate at the base of each corolla lobe, even on the same plant.

By far the largest and most diverse group, sect. ANDICOLA (Griseb.) J. Holub includes most of the Andean species as well as several of Australia and New Zealand. These plants are perennials (occasionally even subligneous

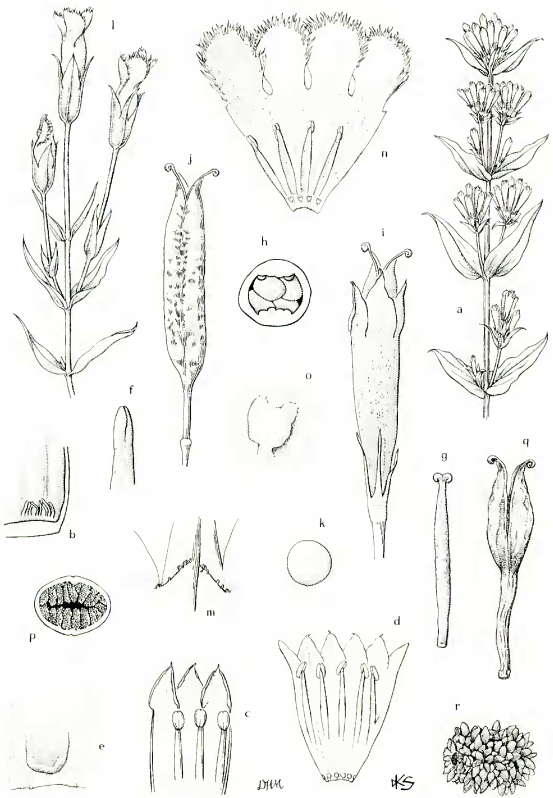

FIGURE 3. **Gentianella** and **Gentianopsis**. a–k, *Gentianella quinquefolia* var. *quinquefolia*: a, upper part of flowering plant, × ½; b, interior of calyx at base of one lobe, showing intracalycine squamellae, × 25; c, three corolla lobes and stamens at anthesis, showing position of anthers, × 3; d, opened corolla, showing glands at base and position of anthers after pollen is shed (cf. "c"), × 2; e, detail of gland at base

ones) or rarely biennials with rotate or salverform corollas. The bases of the filaments and/or the base of the corolla tube is occasionally pilose or barbate. Section ANTARCTOPHILA (Griseb.) J. Holub contains a relatively small number of species restricted to temperate South America, Australia, and New Zealand. These plants are supposedly annuals with rotate, glabrous, efimbriate corollas. These last two sections appear to be heterogeneous and should be reevaluated. The distinction of annual *vs.* perennial habit does not hold, and even *Gentianella montana* (Forster) J. Holub, which was selected by Holub as the lectotype of sect. ANTARCTOPHILA, is a perennial species. The barbate corolla tube and the pilose filaments, used by both Grisebach and Kusnezow to characterize sect. ANDICOLA (although both admitted that neither is constant), are found in relatively few species. Section DASYSTEPHANA Griseb. (not *Dasystephana* Adanson, a genus; see *Gentiana*) contains only *G. thyrsoidea* (Hooker) Fabris, a coarse Peruvian perennial that differs from the above plants principally in that the anthers are basifixed and erect after dehiscence, rather than versatile and pendent. However, several species referable to sect. ANDICOLA in other respects also have erect anthers; this helps to cast doubt on the distinctness of sect. DASYSTEPHANA.

More recently, *Comastoma* (Wettst.) Toyokuni has been segregated from sect. GENTIANELLA—apparently on good evidence. The ten or so species, including the circumboreal *C. tenellum* (Rottb.) Toyokuni, differ from those of *Gentianella* in that there are two epipetalous nectaries per corolla lobe (rather than one) and the fimbriae in the throat of the corolla are united into two nonvascularized scales per corolla lobe (rather than being vascularized, and scattered or united into a continuous ring, if present at all). In addition, those species investigated are $2n = 10$, rather than $2n = 36$, the diploid number characteristic of *Gentianella*. *Comastoma* forms a connecting link between *Gentianella* and *Lomatogonium* A. Br., also with $2n = 10$, and has been united with the latter by several workers.

Chromosome numbers are known for about 30 species in sects. GENTIANELLA, ARCTOPHILA, and ANDICOLA, and all—as pointed out by Weaver and Rüdenberg—are $2n = 36$, with the exception of *G. Moorcroftiana* (Wallich ex Griseb.) Airy Shaw, $2n = 18$ (Mehra & Vasudevan, 1972) and $2n = 26$ (Wada, 1966); *G. auriculata* (Pallas) Gillett, $2n = 48$ (Sokolovskaya, 1968);

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of corolla, × 20; f, stigmatic lobes at anthesis (same stage as in "c"), the lobes not yet receptive to pollen, × 12; g, gynoecium with receptive stigmas, × 3; h, cross section of ovary, showing two placentae, each with two rows of ovules, the two upper ovules visible, × 12; i, mature capsule with marcescent calyx and corolla, × 3; j, open fruit with calyx and corolla removed, × 3; k, seed, × 12. l–r, *Gentianopsis crinita*: l, top of flowering stem (note calyx of two large and two small sepals), × ½; m, interior (adaxial) side of base of one of small sepals, showing intracalycine membrane with squamellae, × 6; n, opened corolla, showing glands at base and stamens, × 1; o, detail of gland from corolla, × 10; p, cross section of ovary, showing placentation, × 6; q, mature capsule, calyx and corolla removed, × 1; r, seed, × 40.

and *G. uliginosa* (Willd.) Borner, $2n$ = ca. 54 (Holmen in Löve & Löve, 1961). The base number is clearly $x = 9$ for the great majority of the species investigated.

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5. **Gentianopsis** Ma, Acta Phytotax. Sinica **1:** 7. 1951.

Annual or biennial [rarely perennial], glabrous [or minutely pubescent], taprooted herbs. Lower leaves arranged in a loose rosette [or rosette dense to absent], attenuate into an indistinct petiole, often withering before anthesis; cauline leaves opposite, sessile, the bases of each pair connected by a transverse line. Flowers 4-merous, large and showy [rarely small], blue or rarely white, long-pedicellate [rarely short-pedicellate to nearly sessile], in few-flowered monochasia or solitary [rarely the plants subscapose], the buds large, ellipsoid, flattened. Calyx persistent, shorter than or equal to the corolla tube, the tube well developed, the lobes [usually] carinate, hyaline margined, the 2 outer ones [usually] plicate, longer and narrower than the inner ones [rarely the lobes nearly equal], each sinus with a thin inner membrane bearing few to many blunt squamellae. Corolla marcescent, broadly funnelform, the tube with 4 cushionlike glands near the base and alternate with the stamens, the lobes dextrorsely contorted in bud, spreading at anthesis, about as long as the tube [or shorter], oblong to spathulate [or orbicular], the margins ciliate in the upper two thirds [more rarely the tips denticulate or the lobes nearly entire]. Stamens included, inserted in the lower half of the corolla tube; filaments with broad [to narrow], lateral, membranaceous wings; anthers distinctly longer than broad, versatile, introrse before dehiscence but bending backward upon dehiscence and appearing extrorse. Stigma with 2 broad, reniform [suborbicular or oblong] lobes; style very short but distinct [rarely absent]; ovary stalked, fusiform, 1-locular, with the numerous ovules covering most of the inner surface. Seeds numerous, oblong [rarely ellipsoid], covered with elongate papillae [rarely seeds reticulate, caudate]. (*Anthopogon* Necker; *Gentiana* L. sect. *Crossopetalum* Froel. ex Griseb.; *Gentianella*

Moench subg. *Eublephis* (Raf.) Gillett.) TYPE SPECIES: *Gentiana crinita* Froel. = *Gentianopsis crinita* (Froel.) Ma.

A genus of 16–25 species distributed throughout most of the boreal and north temperate regions of Eurasia and North America with extensions into the arctic and mountainous areas of the tropics (central Mexico). Although several species are found in the United States, only *Gentianopsis crinita*, $2n = 78$, enters our area. Typical *G. crinita* ranges from central Manitoba, south through the Dakotas and Iowa, and east through the Great Lakes States and southern Quebec to the Atlantic Coast from southern Maine to Maryland and New Jersey, with a few localities along the Appalachians into southwestern North Carolina. Gillett, who included the fringed gentians in *Gentianella* Moench, treated *Gentianopsis Victorinii* (Fern.) Iltis, of the Saint Lawrence Valley, *G. procera* (T. Holm) Ma, of the Great Lakes States, and *G. Macounii* (T. Holm) Iltis, of the prairie areas of the northern United States and Canada, as subspecies of *G. crinita*, but most other authors have considered them to be distinct species.

The fringed gentians form a seemingly natural group, but their proper taxonomic rank has been much debated. Most authors have regarded them as a section of the large, inclusive genus *Gentiana* L. Others have segregated *Gentianella* Moench from *Gentiana* and have included the fringed gentians as a section of that genus. The arguments of Ma and, more recently, Iltis for treating *Gentianopsis* as a distinct genus seem convincing and are accepted here.

Gentianopsis can be separated from *Gentianella*, its closest ally, by a number of characteristics: constant tetramery (*vs.* tetramery or pentamery); squamellate intracalycine membranes at the base of and alternate with the calyx lobes (*vs.* absent); seeds distinctly papillate and generally oblong or angular (*vs.* smooth and globose or slightly flattened); ovules borne over practically the entire inner surface of the ovary (*vs.* borne in two rows along the margins of each suture or rarely in a third row between the sutures); and surface of pollen grains reticulate, with relatively large, angular lumina and adjacent smaller ones (heterobrochate) (*vs.* surface pattern uniformly reticulate, striate, or striate-reticulate).

In addition, the floral vasculature of three species of *Gentianopsis* (*G. crinita, G. detonsa* (Rottb.) Ma, and *G. thermalis* (O. Kuntze) Iltis) has been shown to differ from that of the several species of *Gentianella* studied. In *Gentianopsis* the lateral traces of adjacent calyx segments are fused, as are the ventral traces of adjacent carpels at their origin, although the latter soon become free. In *Gentianella* the adjacent calyx laterals are free, while the adjacent carpel ventrals are fused throughout most of the ovary.

Two widely different chromosome numbers have been reported in *Gentianopsis:* $2n = 44$ for the European *G. ciliata* (L.) Ma and the circumboreal *G. detonsa*, and $2n = 78$ for *G. crinita* and *G. procera*. Doris Löve mentioned, without elaboration, that these groups are "morphologically very well distinguishable" and maintained that "from an evolutionary standpoint it is

very unlikely that both these groups represent the same ancestral line." She therefore suggested that these groups, if segregated from *Gentianella,* be placed in separate genera. Gillett, on the other hand, maintained that *G. crinita* and *G. detonsa* are very close morphologically and that they form a single large species or else two rather weak ones. (He chose the latter alternative in his treatment.) As pointed out by Iltis, very few of the taxa of *Gentianopsis* have been investigated cytologically, and to segregate the *G. ciliata–G. detonsa* and the *G. crinita–G. procera* groups into separate genera on the basis of chromosome number would be premature.

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6. **Frasera** Walter, Fl. Caroliniana, 87. 1788.

Coarse, long-lived monocarpic perennials from a thick taproot [or rather delicate, nonmonocarpic perennials from a woody, horizontal rhizome]. Stems simple, erect, hollow, to 3 m tall [or much shorter in many western American species]. Leaves [opposite or] in whorls of 4 (or 5) [conspicuously white margined], the lower ones tapering to a winged petiole and arranged in a basal rosette, the cauline ones sessile, weakly connate at the base, not decurrent [or the plants subscapose with only a basal rosette]. Inflorescence paniculate, composed of long-pedunculate, modified dichasia arranged in whorls from the upper leaf axils [or dichasia nearly sessile, or rarely the inflorescence a simple terminal raceme or panicle]. Flowers tetramerous. Calyx persistent, deeply divided, the 4 lobes in 2 unequal pairs. Corolla rotate, the 4 lobes united only at the base, greenish-white [bluish], with numerous purplish, blackish, or dark green spots or streaks, each lobe bearing below its middle a large, circular gland conspicuously fringed along its margin [or the gland lunate, linear, deeply bilobed, or tubular] and at its base an inconspicuous, short-fringed coronal scale [or the scale conspicuous and long-fringed or petaloid, or absent]. Stamens inserted in the sinuses of the corolla lobes; filaments subulate-filiform; anthers oblong, reflexing upon dehiscence. Ovary ovate-fusiform, sessile; style filiform, persistent; stigma bilobed, the lobes minute, ovate-orbicular. Capsule flattened parallel to [or rarely opposite] the valves, surrounded by the marcescent corolla and persistent calyx. Seeds dark brown, crescent shaped, finely pitted [or nearly smooth], completely encircled by a membranaceous wing. TYPE SPECIES: *F. caroliniensis* Walter. (Name commemorating John Fraser, 1750–1811, Scottish plant collector and traveler in North America, who published Walter's *Flora Caroliniana*.)—COLUMBO, GREEN GENTIAN.

A genus of about 15 species, with all but one in the mountainous areas of the western United States, often at high elevations. A single species, *Frasera caroliniensis* (*Swertia caroliniensis* (Walter) Kuntze), $2n = 78$, occurs widely in eastern North America. Its distribution is centered in the lower Ohio River valley but extends from Michigan, southern Ontario, and western New York, south to Alabama and Louisiana, and west to eastern Oklahoma. It has been collected in every state in our area except Florida, but only in Tennessee can it be said to be at all common and widespread. It is typically a plant of upland deciduous forests, particularly around their margins and in clearings.

Frasera caroliniensis, as well as several other species, has usually been described as a biennial or triennial. However, Threadgill, Baskin, and Baskin (1981b) recently reported that the plants mature slowly and remain in a rosette stage for an undetermined, but probably prolonged, period. Inouye and Taylor have postulated that in the closely related western American *F. speciosa* Douglas, the minimum age before flowering is 25 to 30 years. Plants of both species die after flowering; most of the species, however, are not monocarpic.

The conspicuous glands on the corolla lobes of all species produce copious nectar. At least *Frasera caroliniensis* appears to be pollinated by several species of bumblebees (*Bombus* spp.). Strong proterandry and the movement of the stamens away from the stigma after dehiscence are adaptations that promote outcrossing.

Frasera is often included in *Swertia* L., the circumscription of which is perhaps the most controversial in the Gentianaceae. It is typified by *S. perennis* L., a plant widespread in alpine areas across much of the Northern Hemisphere, including those in western North America. Perhaps 15 closely related and certainly congeneric species are native to Eurasia. Most modern authors interpret *Swertia* to include *Ophelia* Don, *Stellera* Turcz., and *Anagallidium* Griseb., all restricted to the Old World, and some go so far as to include *Lomatogonium* A. Br. and *Veratrilla* Baillon. The critical characters within the group are plant duration and habit, number of flower parts, number of glands per corolla lobe and morphology of these glands, presence or absence of a style, seed morphology, pollen grain morphology, nodal anatomy, and chromosome number. These groups have not been studied and compared on a world-wide basis since Grisebach's monograph of the family (1845), so overall patterns in the variation or expression of the above characters are not well understood.

Plants of *Frasera* differ most consistently from the other swertioid Gentianaceae in having a distinct, filiform style. In all of the others, the stigma is sessile or nearly so. In addition, the bases of the cauline leaves in *Frasera* are weakly connate and not decurrent, rather than free and decurrent along the length of an internode. The flowers of *Frasera* are always tetramerous, with a single gland per corolla lobe, while those of *Swertia* are usually pentamerous with two glands per corolla lobe. However, several species of *Swertia* are either tetramerous or have a single gland on each corolla lobe.

Nilsson found the pollen of *Frasera* to be morphologically distinct from that of *Swertia*, except for the northern Asian *S. tetrapetala* Pallas. Toyokuni recently transferred this and several other Japanese species to *Frasera*, but this alignment is contradicted by other characters.

Chromosome numbers (all based on 13) have been reported for several *Frasera* species, but only a few species of *Swertia* have been investigated cytologically. The perennial species of *Swertia* (sensu stricto) have numbers mostly based on 14, but 9, 12, and 13 have been reported. *Swertia perennis* itself is variable, with $2n = 18$, 24, and 28. The annual species, sometimes treated in *Ophelia*, have chromosome numbers based on 10, 12, and 13.

The species included in *Frasera* by Card and others form an undoubtedly natural group. In the absence of a modern, comprehensive investigation of the swertioid Gentianaceae, we prefer to maintain them as a distinct genus.

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7. **Obolaria** Linnaeus, Sp. Pl. **2:** 632. 1753; Gen. Pl. ed. 5. 280. 1754, "Obularia."

Low, fleshy, perennial herbs; glabrous except for a few glandular hairs in the axils of the leaves and the sinuses of the corolla; the roots coralloid mycorrhizae. Leaves sessile, purplish, the lower scalelike, the upper spathulate to obdeltoid, the bases decurrent the entire length of the internode, the venation distinct. Flowers sessile or short-pedicellate, usually in 3's or solitary by abortion of the lateral flowers, each group of flowers subtended by a pair of foliaceous bracts. Calyx of 2 free, foliaceous sepals, with a few squamellae on the adaxial side near the base. Corolla imbricate, narrowly campanulate, marcescent, divided nearly to the middle into 4 lobes; tube with inconspicuous, fimbriate scales below the base of each stamen; lobes acute, erose. Stamens 4, inserted at the sinuses of the corolla, equal in length; an-

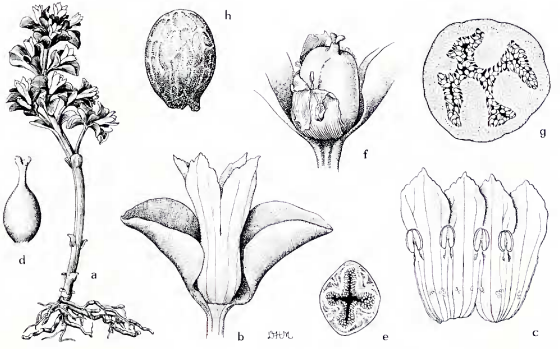

Figure 4. **Obolaria**. a–h, *O. virginica*: a, plant with flowers, × ½; b, flower, × 3; c, corolla laid open to show minute fimbriate scales, introrse anthers, × 3; d, gynoecium, nectariferous tissue not shown, × 3; e, cross section of ovary, × 6; f, nearly mature fruit with marcescent corolla, × 3; g, cross section of nearly mature fruit, × 6; h, seed, × 100.

thers nearly square, dorsifixed, introrse. Ovary sessile, glandular at base, somewhat flattened, 1-locular, the minute ovules very numerous, borne over practically the entire surface of the locule; style short; stigma bilobed, the lobes orbicular, erect, apparently receptive only along the edges. Capsule plump, 1-locular, thin walled, rupturing irregularly. Seeds minute, very numerous, ovoid, minutely striate. (*Shultzia* Raf., 1808; not *Obolaria* Siegesb. ex Kuntze, 1891, = *Linnaea* Gronov. ex L.) TYPE SPECIES: *O. virginica* L. (Name from *obolos*, a small Greek coin, from the fleshy, rounded leaves.)—PENNYWORT.

A single species, *Obolaria virginica* L. (*Shultzia virginica* (L.) Kuntze, *S. obolarioides* Raf.), $2n = 56$, a plant chiefly of moist, shady sites in deciduous forest, distributed from northern New Jersey, west to northern Ohio, southern Indiana, southern Illinois, western Tennessee, southeastern Missouri, and easternmost Arkansas, and south to central Alabama and Georgia and eastern North Carolina, with outlying stations in northern Florida (Jefferson County) and eastern Louisiana (East Feliciana Parish); also reported from Texas. The proterandrous flowers are produced in spring (early March to late May); the seldom-collected fruits mature from late May to early June. The plants are inconspicuous, often barely protruding from the litter on the forest floor, and are easily overlooked.

The generally reduced size of the plants, the purple coloration, and especially the mycorrhizae (which lack root hairs) have led to the suggestion of various degrees of saprophytism or parasitism. However, no haustorial connections with other plants have been found and much chlorophyll is present in the leaves; the plant is thus "able to provide its own starch" (Holm). The physiology has not been studied, and nothing seems to be known of embryology or other details of the life history.

The calyx of *Obolaria*, consisting of two free, foliaceous sepals, is unique among Gentianaceae. The resemblance of the sepals, both in shape and venation, to the leaves and bracts has led some investigators to conclude that *Obolaria* lacks a calyx.

Holm considered the fimbriate scales near the base of the corolla to be nectariferous. However, Lindsey, in his survey of the floral anatomy of the family, found glandular material at the base of the ovary. These macroscopically visible glands are more likely the nectaries.

Decurrent leaf bases are unusual among Gentianaceae. The common condition is for the bases of each pair of leaves (or the petiole bases) to be united, forming a sheath around the stem. The exceptional condition has been noted only in *Obolaria, Bartonia*, and *Swertia*.

The relationships of this well-marked genus are somewhat obscure. *Obolaria* has consistently been most closely associated with *Bartonia*, a genus also characterized by mycorrhizae, the presence of glandular hairs in the axils of the leaves (these also in the corolla sinuses of *Obolaria*), the imbricate vernation of the corolla (in contrast with the usual convolute vernation in other Gentianaceae), and the decurrent (rather than connate) leaf bases. It differs conspicuously, however, in its relatively robust stature, as well as in

having well-developed, characteristic leaves, a calyx of two free, leaflike sepals, inconspicuous fringed scales within the corolla tube, and nectaries at the base of the ovary.

Holm presumed the presence of fimbriate scales on the corolla tube to indicate a relationship with *Swertia*. Nilsson and Skvarla suggested a relationship with the same genus on the basis of pollen-grain morphology, although both Gilg and Kohler had considered the pollen of *Obolaria* to resemble more closely that of *Sabatia, Centaurium,* and *Enicostema* Blume.

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8. **Bartonia** Muhlenberg ex Willdenow, Ges. Naturf. Freunde Berlin Neue Schr. **3:** 444. 1801, nom. cons.[2]

Low, erect (rarely twining) annuals with reduced mycorrhizae, lacking root hairs, presumably partially saprophytic or parasitic. Stems very slender, quadrangular, green to purple, the leaves reduced to minute, opposite to alternate subulate scales with a few glandular hairs at base on adaxial surface. Inflorescence basically of pedunculate dichasia, these terminal and axillary from the upper nodes, sometimes appearing to be racemose by reduction of the lateral dichasia or sometimes reduced to a single flower (especially in *Bartonia verna*). Flowers 4-merous, long-pedicellate. Calyx with a short tube or the 4 lobes nearly free, the 2 outer overlapping the 2 inner. Corolla campanulate, deeply 4-lobed, the lobes imbricate (2 lobes without, 2 within) in bud, each lobe with 1 (in *B. verna*) or 3 veins, greenish yellow, white, or

[2]Conservation superfluous; see Rickett and Stafleu, Taxon **9:** 79. 1960.

pinkish to purplish, marcescent. Stamens 4, alternate with the corolla lobes; filaments short, somewhat dilated, attached at sinuses of corolla lobes; anthers ovate to oblong, mucronate, rounded or emarginate, introrse, frequently deciduous after anthesis, yellow or purple. Gynoecium sessile or somewhat stipitate, the stout style hardly differentiated from the ovary, the 2 stigmas decurrent, usually to top of ovary; ovary oval to elliptic in outline, compressed to quadrangular, unilocular, with numerous minute, 1-integumented ovules covering the entire inner surface on branched, protruding ridges. Fruit a thin-walled, 2-valved capsule, dehiscent along the sutures from the tip or from below the style (thus opening only in the middle). Seeds very numerous, minute, ellipsoid, smooth to minutely reticulate. (*Centaurella* Michaux, 1803; *Centaurium* Pers., 1805, not Hill, 1756; *Agina* Necker ex Post & Kuntze, 1903; not *Bartonia* Sims, 1812, = *Mentzelia* (L.) BSP.) TYPE SPECIES: *B. tenella* Muhl. ex Willd. = *B. virginica* (L.) BSP. (Named for Professor Benjamin Smith Barton, 1766–1815, physician and botanist of Philadelphia, one of the earliest teachers of botany in the United States.)

Three (or possibly four) species, entirely eastern North American in distribution, often of sporadic occurrence, all plants of usually moist, acid soils in peaty, sandy, or sphagnous habitats. The species can be divided into two remarkably distinct groups. Characterized by the combination of early flowering period (November in the south to mid-April in the north), white, one-veined corolla lobes that are three times the length of the calyx, and a capsule opening septicidally below the persistent "style," *Bartonia verna* (Michaux) Raf. ex Barton, $2n = 44$, ranges northward from Broward and Lee counties, Florida, westward on the Gulf Coastal Plain to eastern Louisiana and northward on the outer Atlantic Coastal Plain to southeastern North Carolina (Carteret County).

Both *Bartonia paniculata* (Michaux) Muhl., $2n = 52$, and *B. virginica* (L.) BSP., $2n = 52$, are summer-flowering species (July to late September) with smaller, three-veined corolla lobes up to twice as long as the calyx. Characterized by essentially alternate scale leaves; whitish to purplish, oblong, acute corolla lobes; and a completely two-valved capsule, *B. paniculata* occurs from northern Florida to eastern Texas, northward to Oklahoma, Arkansas, and Kentucky, and especially along the Atlantic Coastal Plain to New England, Nova Scotia, and Newfoundland. It has a single disjunct population in southern Ontario. The southern representative is the more slender, frequently twining, yellow-anthered subsp. *paniculata* (*B. lanceolata* Small), while northward, especially from Rhode Island and Massachusetts to Newfoundland, occurs subsp. *iodandra* (Robinson) Gillett (including vars. *iodandra* (Robinson) Fern., *sabulonensis* (Fern.) Fern., and *intermedia* Fern.), characterized by stouter habit, generally purplish color, and somewhat larger (0.5–1 mm *vs.* ca. 0.5 mm long), usually purple anthers. Gillett noted free intergradation between the subspecies and mapped intermediates from Mississippi, Alabama, and eastern North Carolina, northward to southern Maine and Nova Scotia.

Bartonia virginica, differing in the mostly opposite scale leaves, the greenish yellow, oblong corolla lobes with an apiculate, erose, or entire apex, and

the capsule opening as in *B. verna*, is distributed from central Florida and southern Louisiana, northward to eastern Tennessee, Wisconsin, Michigan, southern Ontario, southern Quebec, and Nova Scotia. The ranges of *B. paniculata* and *B. virginica* overlap in large part; the two sometimes grow together, but usually remain distinct, although putative intermediates have been reported from Mississippi, Alabama, and eastern Virginia, northward to Nova Scotia. Further studies of variation are desirable. (See Gillett.)

Recently an additional species, *Bartonia texana* Correll, has been described from southeastern Texas. This plant reputedly differs from *B. paniculata* in its shorter calyx and corolla, its elliptic and obtuse to obtuse-apiculate (rather than lanceolate and acute or acuminate) corolla lobes, and its capsule usually exceeding (rather than shorter than) the corolla. An isotype, however, suggests that "*B. texana*" may represent merely slightly abnormal populations of *B. paniculata*.

The genus is well marked by the greatly reduced vegetative parts, the tetramerous flowers with imbricate vernation, the peculiar decurrent stigmas, and the numerous minute ovules over the entire surface of the single locule. It is presumably most closely related to *Obolaria* but represents a further stage in specialization. The presence of two types of capsular dehiscence in *Bartonia* is of interest in connection with the distinctions made between *Leiphaimos* and *Voyria*.

All three species are said to be annuals, but little has been recorded of their life histories. On the basis of the coralloid mycorrhizae and greatly reduced leaves, partial saprophytism or partial parasitism has been supposed, although the plants are green and the habitat is a peculiar one for a saprophytic existence. No haustorial connections with other vascular plants have been found, but the possibility of parasitism via a fungal "bridge" (as demonstrated in *Monotropa*; see Furman & Trappe) should be investigated.

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9. **Eustoma** Salisbury, Paradisus Londinensis **1:** *pl. 34*. 1806.

Glaucous, erect, annual or perennial, taprooted herbs, usually of somewhat calcareous or alkaline open habitats. Leaves opposite, sessile, more or less clasping, palmately veined. Flowers large, long-pedicellate, in few-flowered monochasia. Calyx persistent, longer than the corolla tube, the tube short, the 5 (or 6) lobes long-acuminate, keeled abaxially. Corolla showy, blue-purple, rose-purple, violet, pink, white, or rarely yellow, campanulate-fun-

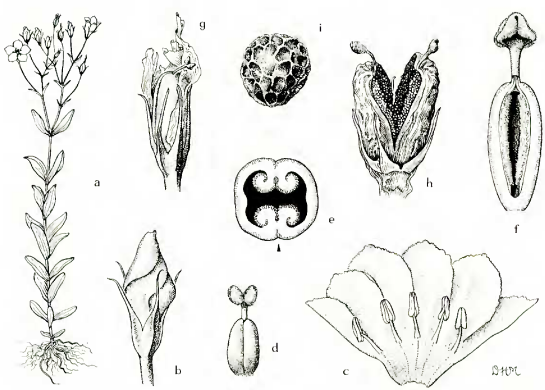

FIGURE 5. **Eustoma**. a–i, *E. exaltatum*: a, small plant in flower, × ⅛; b, flower bud, × 1; c, corolla laid open to show contorted imbrication and epipetalous stamens, × 1; d, gynoecium, × 1; e, cross section at middle of ovary, × 3; f, gynoecium, the ovary in vertical section, position indicated by arrow in "e," × 2; g, nearly mature capsule with marcescent corolla, × 1; h, mature fruit, showing dehiscence and numerous seeds on four placentae, × 2; i, seed, × 50.

nelform, marcescent, dextrorsely contorted in bud, the 5 (or 6) lobes ascending, longer to much longer than the broadly campanulate tube. Stamens 5 (or 6), inserted in the throat of the corolla below the sinuses; filaments slender; anthers versatile, oblong, longitudinally dehiscent, extrorse, straight, not recurving. Stigma with 2 broad, oval to suborbicular lobes; style slender, shorter than to as long as the ovary, the base persistent; ovary 1-locular with 2 bilamellate, parietal, weakly projecting placentae with very numerous ovules, glandular at base, but the glands not macroscopically discernible. Capsule oblong or ovoid, 1-locular, 2-valved, dehiscent through the placentae. Seeds minute, very numerous, globose, densely pitted, detaching from the persistent funiculi on the placentae. (*Dupratzia* Raf.) TYPE SPECIES: *E. silenifolium* Salisb. = *E. exaltatum* (L.) Salisb. ex G. Don. (Name from Greek, *eustomos*, "a beautiful mouth," or "of good countenance," alluding to the beautiful throat of the corolla).

Three species, two partly in our region, the third, *Eustoma Barkleyi* Standley ex Shinners, apparently known only from a limited area in Coahuila, Mexico. *Eustoma exaltatum*, catch-fly gentian, ranges from the Greater Antilles to the Bahamas and into coastal areas, open pinelands, coastal sand dunes, and openings in hammocks of southern and central Florida, southern Mississippi, and southern Louisiana; thence across southern Texas, and sporadically inland in calcareous or alkaline soils through New Mexico to southern California, and south through Mexico and Central America into Venezuela. *Eustoma grandiflorum* (Raf.) Shinners (*E. Russellianum* (Hooker) G. Don ex Sweet), Texas bluebell, prairie gentian, is a showier, larger-flowered plant (corolla lobes 2.5–5 cm long *vs.* 1.4–2.6 cm), of more inland range, from southern Texas and northern Mexico to New Mexico, Utah, Wyoming, Colorado, Nebraska, Kansas, and Oklahoma. A single collection has been reported by Moore from Arkansas (Arkansas County). Shinners suggested "very extensive introgression between the[se] two most wide-ranging species where their ranges overlap in southern Texas," as well as between *E. grandiflorum* and *E. Barkleyi*, and pointed to the desirability of a detailed genetic and biometric study of the genus. A number of color forms (see Shinners) have been distinguished in *E. grandiflorum*, which merits more frequent cultivation. Both single- and double-flowered forms of this species are grown in Japan for cut flowers.

The affinities of *Eustoma* have been the subject of some debate. Grisebach did not treat the genus at all in his *Genera et Species Gentianearum* (1839) but later (1845) included it in his tribe Chloreae, next to *Sabatia*. The basic character used in delimiting the Chloreae was the presence of a completely deciduous style, even though the base of the style in *Eustoma* is persistent. Bentham and Hooker placed *Eustoma* in the tribe Chironeae, subtribe Lisiantheae, with five other genera, all restricted to the American tropics. Characters used to delimit this subtribe included the presence of a bilamellate stigma and a persistent style. Gilg treated the genus in his tribe Gentianeae, subtribe Tachiinae, with six neotropical genera (including several associated with it by Bentham and Hooker) in addition to the Malagasyan genus *Tach-*

iadenus Griseb. Gilg's tribes and subtribes were delimited primarily on the characters of the pollen grains, and Gentianeae-Tachiinae were characterized by having single grains (monads) with a reticulate exine pattern.

Work since Gilg's time has more or less supported his placement of *Eustoma*. Chromosome numbers reported for *E. exaltatum*, $2n$ = ca. 72, and *E. grandiflorum*, $2n$ = 72, support a relationship with *Lisianthius* P. Br. (nine species with $2n$ = 36), one of its closest relatives in Gilg's system. According to Lindsey, the vascular anatomy of the flowers of *Eustoma* supports its inclusion in the Gentianeae-Tachiinae, but he noted that it appears to be the least specialized member of the group. Lindsey also reported the presence of glandular tissue at the base of the ovary. These glands, however, are not macroscopically discernible, whereas other genera in Gilg's Gentianeae-Tachiinae have a well-developed glandular disc at the base of the ovary. It seems that *Eustoma* is somewhat transitional between *Gentiana* and its relatives in Gilg's Gentianeae subtribe Gentianinae, and *Lisianthius* and other genera associated with it in the Gentianeae subtribe Tachiinae.

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10. **Voyria** Aublet, Hist. Pl. Guiane Fr. **1:** 208. 1775.

Small, erect, presumably saprophytic herbs with mycorrhizae, lacking chlorophyll. Leaves opposite, scalelike, usually small and inconspicuous. Flowers in terminal cymose inflorescences [or solitary], ebracteate or 1[–3]-bracteate, usually 5-merous. Calyx of 5 [rarely 4 or 6] lobes, persistent [or deciduous], much shorter than the corolla tube, often with 5 glandlike structures within, these probably representing fused masses of calycine squamellae. Corolla white or pinkish [yellow, orange, blue, rose, or reddish purple], usually salverform [or rarely clavate], with a long tube, [4 or] 5 [or 6]-lobed [the lobes rarely reduced to teeth], lobes contorted in aestivation, corolla marcescent. Anthers nearly sessile [or filamented], introrse, sometimes connate, the base of each half [obtuse, acute, or] more or less elongated into a subplumose bristle; pollen very small, [circular to oval or irregular in polar view, in lateral view convexo-concave, or convexo-plane to ovate-flattened], 1–3-porate. Stigma peltate [or capitate], bilobed; style usually distinct, filiform, short [or long], persistent; ovary spindle shaped [or ovoid and sometimes with 2 stalked nectaries at the base], 1-locular, the 2-lobed placentae parietal along the sutures, the ovules very numerous, [anatropous, 1-integumented] to much reduced, straight, and without a distinguishable integument. Capsule surrounded by the persistent membranaceous corolla, 2-valved, fenestrate (dehiscing in the middle, not at base and apex) [or completely 2-valved from the apex]. Seeds numerous, small, spindle shaped with threadlike tails [or globose, sometimes winged], with a few endosperm cells and rudimentary embryo; in ours, sterile ovules developing into scattered hairlike structures ("paraphyses") persistent on the placentae. (Including *Leiphaimos* Schlecht. & Cham. Linnaea **6:** 387. 1831. Type species: *L. parasitica* Schlecht. & Cham.) LECTOTYPE SPECIES: *V. rosea* Aublet.[3] (Local name for these plants in French Guiana; "elle est nommée Voyria par les Garipons.")

About 30 species (placed in six sections by Progel), centered in the lowland forests of tropical Central and South America, but also in the West Indies, with one (*Voyria primuloides* Baker) in West Africa. The northernmost, and one of the most widespread species, *V. parasitica* (Schlecht. & Cham.) Ruyters & Maas (*Leiphaimos parasitica* Schlecht. & Cham., *V. mexicana* Griseb.), of sect. LEIPHAIMOS Griseb., is primarily of the Bahamas, Cuba, Hispaniola, Jamaica, southeastern Mexico, and Honduras, but reaches the extreme south of our area in hammocks of subtropical Florida (Dade and Monroe counties). The species is easily recognizable by the small, whitish flowers arranged in open cymose inflorescences.

[3]Although the general practice in these treatments has been to avoid the designation of lectotype species, which are more appropriately chosen by monographers, in this instance the choice seems clear: Aublet's genus is based largely on *Voyria rosea*, which is much more fully described and is illustrated in greater detail than *V. caerulea* Aublet (noted as "altera species"). In this we disagree with Raynal (Adansonia II. **7:** 64. 1967), who instead chose *V. caerulea* without discussion.

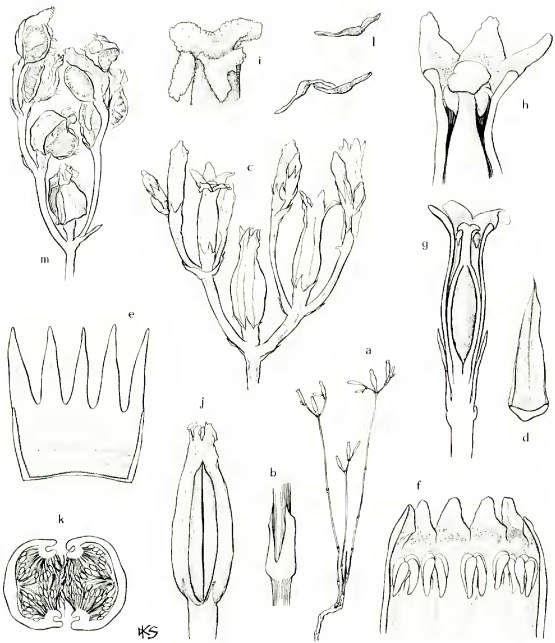

FIGURE 6. **Voyria** (*Leiphaimos*). a–m, *V. parasitica*: a, plant with flowers and immature capsules, × ½; b, stem node, showing perfoliate leaf-pairs, × 6; c, inflorescence with buds, flowers, and developing fruits, showing cymose arrangement, × 3; d, adaxial surface of inflorescence bract, showing position of basal gland (densely stippled area), × 12; e, calyx laid open to show glandlike structures (probably representing fused masses of squamellae), × 24; f, upper part of corolla laid open to show reflexed anther halves, × 12; g, flower in vertical section, × 12; h, detail of upper part of flower (part of corolla removed), showing relationship of anthers to stigma, × 12; i, stigmas with two adherent, flaplike pollen masses below, × 25; j, mature but undehisced capsule partly enclosed by persistent corolla, × 6; k, cross section of dehiscing capsule, showing parietal placentation, dehiscence occurring between the placentae (many seeds and paraphysislike hairs omitted), × 12; l, seeds, membranaceous seed coat elongated as wings (or tails), × 25; m, infructescence of dehisced capsules, showing hairs along suture margins, × 3.

Members of this curious genus, all of which have mycorrhizae and lack chlorophyll, have been supposed to be saprophytes dwelling in humus, fallen leaves, and decaying wood, but parasitism has also been suggested, and it is most likely that members of *Voyria* (and *Voyriella* Miq.) are parasites of the *Monotropa* type (see Furman & Trappe). The species of *Voyria* are notable for their wide range in corolla size, color, and shape; diversity in anther shape, appendages, filaments, and connation; variation in inflorescences, calyx, and nectar glands at the base of the ovary and within the calyx; and extreme reduction of embryo and endosperm.

The genus is here maintained in the sense of Progel (its most recent monographer) and of Bentham and Hooker, rather than that of Gilg, who restricted *Voyria* to a group of about six species, mostly with thick, fleshy mycorrhizae, relatively large flowers, completely bivalved capsules that open from the top, and slightly convexo-concave pollen with two "polar" germ pores. Gilg maintained *Leiphaimos*, of which ours is the type species, for those species with more delicate mycorrhizae, smaller flowers, capsules that open only in the middle (the valves above and below remaining united), and ovoid pollen with a single apical pore. Badly overemphasizing incompletely studied pollen characteristics, he even assigned the two genera to different tribes.

The supposed differences, however, appear to be inconsistent. There seems to be no discontinuity in the degree of vegetative development or in the size of the flower (corolla length 3.5–11 cm in *Voyria vs.* 1–4.5 cm in *Leiphaimos*). The number of bracts (used by Jonker, 1936b) varies from three to none, often depending upon the position of a flower in the inflorescence. Although the manner of dehiscence of the capsule is often characteristic, it should be noted that the capsules of many species are unknown, and Splitgerber described and illustrated that of a *Leiphaimos* (his *V. aurantiaca*) with a completely 2-valved capsule. Both types of dehiscence occur in *Bartonia*, the species of which are likewise much reduced vegetatively. Both "bent" and "straight" pollen sometimes occur in the same flower (Jonker, 1936a; however, cf. Nilsson & Skvarla), and the number and size of pores vary. Erdtman commented, "Pollen morphology does not argue in favor of ± pronounced differences (cf. Svedelius 1902) between *Leiphaimos* and *Voyria*. A parallel to the partial aperture reduction in (these) genera is found in Apocynaceae (*Landolphia* sect. *Saba*)." Nilsson and Skvarla agreed that neither the pollen shape nor the number of apertures is stable enough to differentiate *Leiphaimos* as a genus distinct from *Voyria*.

More recently, Raynal has suggested that *Leiphaimos* be restricted to the type species, *L. parasitica*. The supposedly unique characteristics of this species are its scorpioid inflorescence and its peculiar stigma, which Raynal described as bilobed with a pendent, glandlike flap on both sides between the lobes. However, our own observations have shown that the inflorescences of *Voyria parasitica* are commonly normal compound dichasia, rather than scorpioid ones. In addition, the anthers dehisce directly against the stigma, and the stigmatic flaps reported by Raynal are merely coalesced masses of germinated pollen grains (FIGURE 6, i).

Williams divided the Central American saprophytic gentians between *Lei-*

phaimos and *Voyria*, using characters of the capsule and seeds to distinguish the two. According to him, species with wingless ovoid or trigonous seeds and no elaterlike hairs (paraphyses) within the capsule belong to *Voyria*, while those with flattened, winged or appendaged seeds, and elaterlike hairs within the capsule belong to *Leiphaimos*. Although these characters may yet prove to be important, the South American species were not included in Williams's study. Elias and Robyns found the conclusions of Raynal and of Williams contradictory and combined *Voyria* and *Leiphaimos* in the *Flora of Panama*.

Altogether, the combinations of characters are reticulate, and in the absence of a modern and balanced monograph, the generic treatment of these imperfectly known plants followed by most authors previous to Gilg seems the most reasonable. The relationships of *Voyria* to other Gentianaceae are not clear. Most authors have considered the genus to be closely allied to *Voyriella* Miq., a bitypic, achlorophyllous, mycotrophic South American genus, but recent evidence, particularly palynological, argues against such a relationship (Nilsson & Skvarla).

Few species have been studied embryologically. A variety of seed types occur, and a reduction series from anatropous, one-integumented ovules to apparently straight ovules with no distinguishable integument is indicated. The megagametophyte appears to be of the Polygonum type. Both endosperm and embryo are much reduced, reaching an extreme of three and two cells, respectively. The chromosome number of "*Leiphaimos azurea*" (*L. azurea* (Karsten) Gilg = *V. tenella* Hooker, according to Jonker, 1936b) has been reported as $2n = 36$.

Aublet said that the fleshy rhizomes of *Voyria rosea* and *V. caerulea* were eaten by the Indians of French Guiana.

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